OXFORD

Forest Entomology

Bivariate Pheromone-based Monitoring of Spruce Budworm Larvae (Lepidoptera: Tortricidae)

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Abstract

A bivariate approach to pheromone-based monitoring is developed for the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). The approach uses captures of males at pheromone traps for generation t ($\male_t$) as a transitive term between densities of overwintering larvae in consecutive generations ($L2_t$, $L2_{t+1}$), based on a large data set including >2,000 observations in the province of Quebec (QC) between the interval 1992 and 2010. Although estimates of $L2_t$ and $\male_t$ are autocorrelated to some extent, multi-year assessments of larval densities combined with pheromone trapping are justified by the complementarity (statistical significance) of both $L2_t$ and $\male_t$ in predicting $L2_{t+1}$ for 15 of 18 pairs of 2-yr intervals. Bivariate pheromone-based thresholds (number of males corresponding to specific transitions in larval densities between $L2_t$ and $L2_{t+1}$) are reported for each year. As expected, thresholds for stable populations ($L2_t = L2_{t+1}$) were lower than for populations with positive growth rate ($L2_t < L2_{t+1}$). The thresholds derived in this study have limited heuristic value; however, because they vary greatly from year to year.

Key Words: eruptive population dynamics, forest defoliator, multivariate function, pheromone-based threshold, pheromone quality control

Traps baited with moth sex pheromones have become an integral part of monitoring programs of forest defoliators, either as surveillance (detection of areas where insect populations may become problematic) or a forecasting tool (prediction of local population density) (Grant 1991, McNeil 1991, Witzgall et al. 2010, Evenden and Silk 2015). The integration of pheromone trap data into sampling plans is often limited by poor correlations between numbers of males at pheromone traps ($\male_t$) and subsequent density of larvae (L_{t+1}), as well as variable year-to-year relationships (Sweeney et al. 1990, Carter et al. 1992, Lyytikäinen-Saarenmaa et al. 1999, Morewood et al. 2000, Jactel et al. 2006). The accuracy of pheromone monitoring might be improved by taking into account larval densities in parental generations [$L_t \rightarrow \male_t \rightarrow L_{t+1}$]. This dual approach has often been used (Shepherd et al. 1985, Evenden et al. 1995, Morewood et al. 2000, Asaro and Berisford 2001, Jones et al. 2009), but sample sizes are generally too low (in terms of year or location) to determine whether and to what extent pheromone trapping improves forecasting of larval abundance.

The potential application and challenges of combined larval–adult monitoring are explored for the spruce budworm, *Choristoneura fumiferana* Clem. (Lepidoptera: Tortricidae) (henceforth designated as budworm), a univoltine defoliator of balsam fir (*Abies balsamea* (L.) Mill.) and spruces (*Picea* spp.) in eastern North American boreal forests (Morris 1963). After eggs hatch in the fall,

non-feeding first instars seek microsites to construct a hibernaculum to overwinter as second instars (L2), then larvae resume development the following spring. Larvae feed preferentially on current-year shoots, and the majority of defoliation is caused by penultimate sixth instars. Shortly after emergence in July, females release sex pheromone (95:5 *E:Z*-11 tetradecenal) to attract males and, upon mating, lay clusters of eggs on host trees (Silk et al. 1980, Silk and Kuenen 1988, Rhainds et al. 2012).

Captures of male budworms at pheromone traps have long been used to forecast larval densities, although initial attempts were limited by the lack of uniform lures and trap designs (Houseweart et al. 1981, Ramaswamy et al. 1983, Allen et al. 1986, Sanders 1988). The availability of standardized commercial lures (Biolure®; Suterra Inc., Bend, OR) and traps (Multi-Pher; Distributions Solida, Saint-Férréol-Les-Neiges, QC) since the 1990s has facilitated the development of pheromone-based thresholds (Lyons et al. 2000, 2002; Rhainds et al. 2016). The Biolure product was discontinued in 2010; it has since been replaced by Flexlure (Contech Enterprises Inc., Victoria, BC). Unfortunately, the relative attractiveness of these two lures was not compared across a wide range of budworm densities, which created a 'rupture' in the time series of moth abundance.

The long-term data set generated in the province of Quebec (QC) since 1993 has considerable heuristic value, due to the large number

(thousands) of sites that include estimates of densities of overwintering larvae in consecutive generations (L2$_t$, L2$_{t+1}$) as well as numbers of males captured at pheromone traps (♂$_t$). The interval 1993–2010 in QC encompasses the transition phase from endemic to epidemic populations (Bouchard and Auger 2014) and, as such, provides comparative or reference material for jurisdictions where budworm populations are on the cusp of an outbreak.

Population dynamics of budworms are characterized by synchronous outbreaks that coincide in time and space, with a periodicity of 35–40 yr (Royama 1984, Boulanger and Arsenault 2004, Sturtevant et al. 2015). The negative economic impact of budworm is due to the vast geographic extent of outbreaks (50 million ha in the 1970s; Sturtevant et al. 2015) combined with the severe effect of defoliation on host trees (reduced growth and mortality) (MacLean 1984). The most recent outbreak now encompasses >7 million ha of defoliated forests in QC, including areas near the northwest border of New Brunswick (Ministère des Forêts, de la Faune et des Parcs 2016). The cost associated with budworm infestations is staggering: if left unchecked, the impending outbreak in NB *alone* is expected to reduce economic output by CND $3.3–4.7 billion (Chang et al. 2012).

Early intervention strategy (EIS) is currently implemented in NB to alleviate negative consequences of the expected outbreak. This proactive approach aims at preventing populations from reaching epidemic levels by treating 'hot spots' to re-establish low-density equilibrium with natural enemies and limit moth migration (Régnière et al. 2001). Logistically, EIS is achieved through aerial application of microbial insecticide (*Bacillus thurigiensis kurstaki*; Fournier et al. 2009) or insect growth regulator (tebufenozide, or Mimic; van Frankhenhuyzen and Régnière 2017).

The objective of this study is to derive pheromone-based thresholds corresponding to specific transitions of larval densities between years, within a range of density relevant to EIS (two to six L2 per branch; Régnière et al. 2001, Rhainds et al. 2016).

Materials and Methods

Sampling Procedure

The study is part of an ongoing survey initiated in the province of QC in 1992 to monitor the local abundance of budworm. The survey includes several hundred sites every year, with each site consisting of forest stands with preferred hosts of budworm (balsam fir and spruces) as dominant or co-dominant tree species. We analyze a subset of the data collected in balsam fir stands sampled over consecutive years and for which three parameters are available: 1) L2$_t$ = number of second instars per branch in generation t; 2) ♂$_t$ = number of males per pheromone trap in generation t; and 3) L2$_{t+1}$ = number of L2 per branch in generation $t+1$. Sample sizes (number of sites) for different years are reported in Table 1. Even though the univoltine life cycle of budworm spans over 2 yr (L2 overwinter in year t and resume feeding in year $t + 1$), we retain the notation above because males captured in year $t + 1$ belong to a generational cohort of budworms that initiated development the previous year.

Larval sampling was conducted with a standardized procedure over the course of the study. Branches were pruned from the upper midcrown of balsam firs (three branches collected on different trees for most sites, up to nine branches at some sites between 1993 and 2002). The 75-cm apical section of each branch was placed in individual plastic bags and brought to the laboratory to extract L2 from their hibernacula with a solution of 1.5% sodium hydroxide

Table 1. Parameters of bivariate exponential regressions describing relationships between densities of overwintering spruce budworm larvae over consecutive years (L2$_t$ and L2$_{t+1}$) in combination with numbers of males captured at pheromone traps (♂$_t$): ln (L2$_{t+1}$ +1) = β_0 + β_1 ln (L2$_t$ +1) + β_2 × $k^{\ln(\sigma t +1)}$ (equation 1 in text); the k value was set at 1.7

Year, t	N	β_0	β_1	β_2	r^2
1992	107	0.0796	0.6462***	0.0341***	0.705***
1993	111	0.1087*	0.3230***	0.0597***	0.770***
1994	109	0.0498	0.7292***	0.0270*	0.740***
1995	109	–0.1052	0.0928	0.1213***	0.832***
1996	101	–0.0577	0.3870***	0.0714***	0.836***
1997	104	–0.1034*	0.6941***	0.0447***	0.808***
1998	105	–0.1027*	0.4545***	0.0275**	0.772***
1999	115	–0.1530*	0.2510*	0.0727***	0.689***
2000	113	–0.1217**	0.2250**	0.0631***	0.804***
2001	68	–0.0092	0.5084**	0.0800**	0.784***
2002	57	–0.2074**	0.7453***	0.0771**	0.831***
2003	101	–0.1323	0.4462***	0.0456***	0.787***
2004	94	0.0794	0.2504*	0.0023	0.127**
2005	99	–0.0583	0.2232	0.0237***	0.257***
2006	112	–0.0131	0.6224***	0.0368***	0.609***
2007	222	–0.1088*	0.5498***	0.0456***	0.671***
2008	164	–0.0526	0.8104***	0.0406***	0.758***
2009	240	0.0244	0.5641***	0.0574***	0.592***

***P < 0.0001; **P < 0.001; *P < 0.05.

(Rhainds et al. 2016). Sampling was always conducted in the fall (rather than following spring) to prevent bias in density assessments due to overwintering mortality.

Non-saturating Multi-Pher traps (Jobin and Coulombe 1988) baited with pheromone (Biolure, 2.8 mg load of pheromone released from a permeable membrane) were used to capture male budworms [three traps per site] (Rhainds et al. 2016). Pheromone traps were deployed in the upper tree canopy (TC) of balsam fir at all sites between 1993 and 2001, and on low branches at ground level (GL) or TC between 2002 and 2010; the objective of shifting position from TC to GL was to facilitate the field deployment of traps. Captures of males at pheromone traps strongly correlate with densities of L2 independent of trap position, and the highly significant (P < 0.0001) relationships between captures at TC and GL do not vary between years (Rhainds et al. 2016). In the context of future prognostics of budworm abundance (which will be based on traps at ground level), estimates of male density at TC were converted to GL using the equation ln ♂$_{GL}$ = (1.127 × ln ♂$_{TC}$) – 1.786 (Rhainds et al. 2016).

Statistical Analysis

Analyses were conducted with SAS (SAS Institute Inc., Cary, NC). Larval and moth counts were subjected to logarithmic transformations [$x' = \ln(x + 1)$] to reduce heterogeneity of variance. Relationships between densities of L2 and moths (using average values pooled across sites, on a per year basis) were evaluated with linear regressions. For all other analyses, the experimental unit of observation consisted of observed values (L2$_t$, ♂$_t$, L2$_{t+1}$) at any given site and year.

Relationships between ♂$_t$ and L2$_{t+1}$ were modeled with exponential regressions ln L2$_{t+1}$ = β_0 + β_1 × $k^{\ln(\sigma t +1)}$ (Rhainds et al. 2016); standardized value of k was assessed by pooling data across years. The iterative selection process relied on a comparison of exponential models with different estimates of k (using one decimal point intervals); the k value that yielded the highest coefficient of determination

$(k = 1.7, r^2 = 0.5182)$ was retained in subsequent analyses. Multiple iterations demonstrated that the derivation of pheromone-based thresholds is largely insensitive to k values. Bivariate regressions were solved separately for each year:

$$\ln(L2_{t+1} + 1) = \beta_0 + \beta_1 \ln(L2_t + 1) + \beta_2 \times k^{\ln(\sigma t)} \quad (1)$$

Bivariate models were used to estimate pheromone-based thresholds σ_t (number of males per trap corresponding to predetermined values of n $L2_{t+1}$ and $L2_t$); the equation was solved separately for each year t.

$$\sigma_t^* = \exp\left\{\frac{\ln\left[\ln\left(L2_{t+1} + 1\right) - \beta_0 - \beta_1 \ln\left(L2_t + 1\right)\right] - \ln\left(\beta_2\right)}{\ln(k)}\right\} - 1 \quad (2)$$

Equation 2 was solved for values of n $L2_{t+1}$ constrained between 2 and 5, using increment of one individual per branch between $L2_t$ and $L2_{t+1}$ (from $L2_t = 0$ to $L2_t = L2_{t+1}$). Pheromone-based thresholds were bounded within 600 males because few observations exceed that value (50 of 2131 observations, or 2.3%); male thresholds for $L2_{t+1} = 6$ were not derived because most estimates exceeded 600. Pheromone-based thresholds were not reported for years with most threshold estimates exceeding 600 males (1998–1999, 2004–2005, 2005–2006). Parameters of bivariate regressions used to solve equation 2 are reported for each year in Table 1.

Results

The data set included 2131 observations spanning 18 yr (between 57–240 sites per year) (Table 1). Overall, captures of moths (σ_t, averaged on a per year basis by pooling data across sites) were not significantly related to densities of larvae, neither for $L2_t$ and $L2_{t+1}$ (Fig. 1).
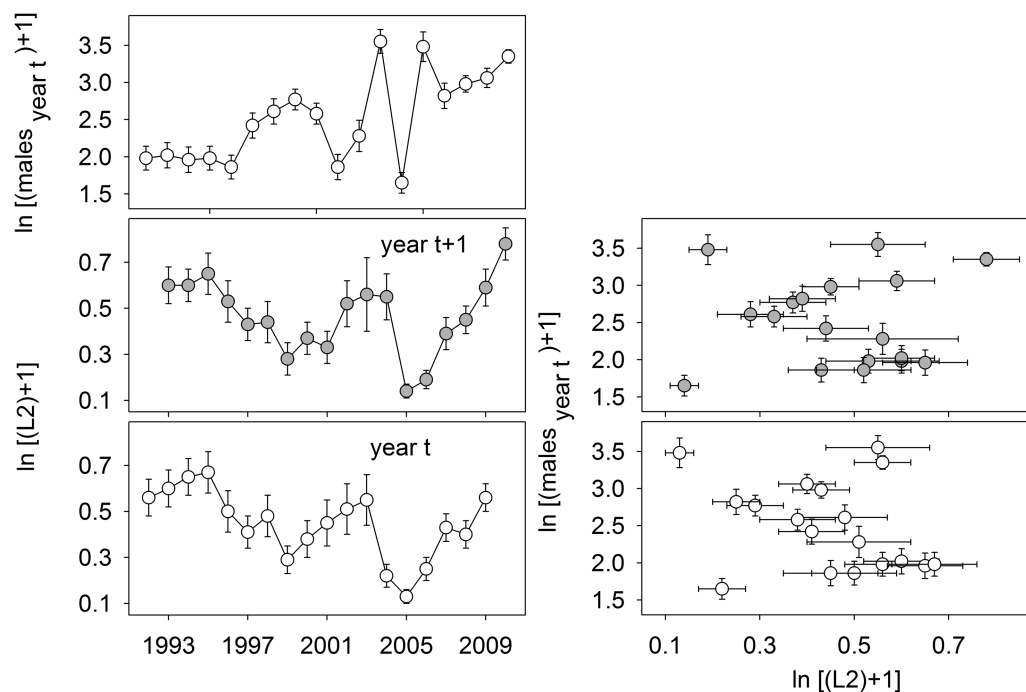
On a per year basis, in contrast, exponential regressions of the form $\ln L2_{t+1} = \beta_0 + \beta_1 \times k^{\ln(\sigma t + 1)}$ were significant for each one of eighteen 2-yr intervals (Fig. 2).

A generalized linear model factoring the effect of year on bivariate regressions (equation 1) revealed highly significant relationships between $L2_{t+1}$ and both $L2_t$ ($F = 392.95$, df = 1, 2077, $P < 0.0001$) and σ_t ($F = 309.73$, df = 1, 2077, $P < 0.0001$), with significant year effects (Year: $F = 2.20$, df = 17, 2077, $P = 0.0032$; Year × $L2_t$: $F = 6.34$, df = 17, 2077, $P < 0.0001$; Year × σ_t: $F = 6.42$, df = 17, 2077, $P < 0.0001$). The coefficient of determination of models including year effects ($r^2 = 0.728$) was only 5.2% more accurate than models including only $L2_t$ and σ_t ($r^2 = 0.676$).

Due to significant year effects, parameters of bivariate regression models were solved separately for each of eighteen 2-yr intervals, as reported in Table 1. Larval density in parental generations ($L2_{t+1}$) was significantly correlated with both $L2_t$ and σ_t for 15 of 18 2-yr intervals (Table 1).

Average values of pheromone-based thresholds (on a per year basis) corresponding to larval transitions from $L2_t = 0$ to n $L2_{t+1}$ were as follows: for $n = 2$: 356 σ; $n = 3$: 430 σ; $n = 4$: 476 σ; $n = 5$: 517 σ (Fig. 3).

Thresholds corresponding to stable larval populations ($L2_t = L2_{t+1}$) were 2.5–4.0 times lower than those associated with transitions $L2_t = 0 \rightarrow n$ $L2_{t+1}$, and averaged 87 σ for $n = 2$, 130 σ for $n = 3$, 169 σ for $n = 4$, and 205 σ for $n = 5$ (Fig. 3).

In comparison with models $L2_t = 0 \rightarrow n$ $L2_{t+1}$ and $L2_t = L2_{t+1}$, intermediate thresholds were observed for the range $0 < L2_t < L2_{t+1}$ (Fig. 3).

Discussion

Annual variations in relationships between captures of moths at pheromone-baited traps and larval densities restrict the predictability and reliability of pheromone-based monitoring (Fig. 2 in Sanders 1988; Fig. 1 in Hillier et al. 2004; Fig. 1 in Mori et al. 2014). In
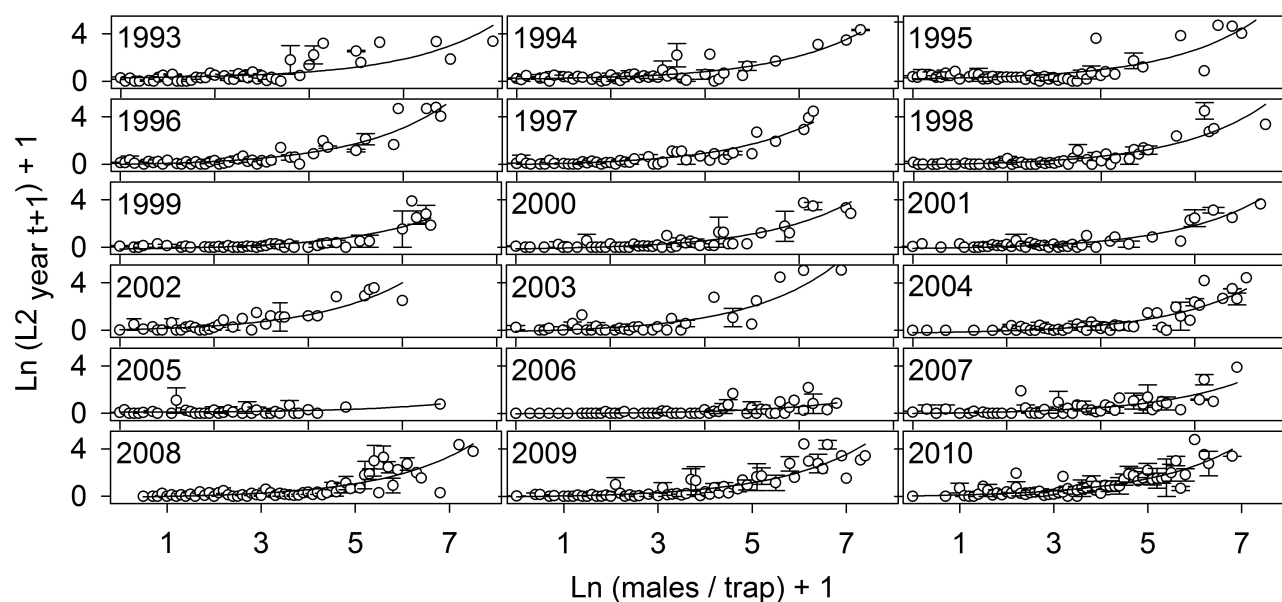

Fig. 1. Variation in densities of spruce budworm overwintering larvae (L2) and males captured at pheromone-baited traps over a 18-yr interval between 1992 and 2010. Relationships between males and L2 were not significant in year t ($L2_t \sim \sigma_t$; $r^2 = 0.089$, $P = 0.2280$) or $t+1$ (($L2_{t+1} \sim \sigma t$; $r^2 = 0.001$, $P = 0.9162$).

Fig. 2. Relationships between the average number of male spruce budworms at pheromone-baited traps ($\male_t$) and the density of overwintering larvae ($L2_{t+1}$) per 75-cm branch sections in of balsam fir. For each year, the solid lines represent exponential regressions modeled with the function $\ln L2_{t+1} = \beta_0 + \beta_1 \times k^{\ln(\male t+1)}$ (with k set at 1.7). Parameters of regressions are as follows: 1993: $\beta_0 = 0.285$, $\beta_1 = 0.066$, $r^2 = 0.426$, $P < 0.0001$; 1994, $\beta_0 = 0.193$, $\beta_1 = 0.082$, $r^2 = 0.701$, $P < 0.0001$; 1995: $\beta_0 = 0.173$, $\beta_1 = 0.123$, $r^2 = 0.559$, $P < 0.0001$; 1996, $\beta_0 = -0.090$, $\beta_1 = 0.131$, $r^2 = 0.829$, $P < 0.0001$; 1997, $\beta_0 = -0.101$, $\beta_1 = 0.128$, $r^2 = 0.788$, $P < 0.0001$; 1998, $\beta_0 = -0.122$, $\beta_1 = 0.097$, $r^2 = 0.698$, $P < 0.0001$; 1999: $\beta_0 = -0.212$, $\beta_1 = 0.080$, $r^2 = 0.685$, $P < 0.0001$; 2000, $\beta_0 = -0.209$, $\beta_1 = 0.093$, $r^2 = 0.676$, $P < 0.0001$; 2001: $\beta_0 = -0.150$, $\beta_1 = 0.082$, $r^2 = 0.780$, $P < 0.0001$; 2002, $\beta_0 = -0.120$, $\beta_1 = 0.171$, $r^2 = 0.732$, $P < 0.0001$; 2003: $\beta_0 = -0.242$, $\beta_1 = 0.158$, $r^2 = 0.756$, $P < 0.0001$; 2004, $\beta_0 = -0.287$, $\beta_1 = 0.087$, $r^2 = 0.702$, $P < 0.0001$; 2005: $\beta_0 = 0.073$, $\beta_1 = 0.021$, $r^2 = 0.007$, $P < 0.05$; 2006, $\beta_0 = -0.046$, $\beta_1 = 0.026$, $r^2 = 0.228$, $P < 0.0001$; 2007: $\beta_0 = -0.070$, $\beta_1 = 0.068$, $r^2 = 0.451$, $P < 0.0001$; 2008, $\beta_0 = -0.155$, $\beta_1 = 0.086$, $r^2 = 0.499$, $P < 0.0001$; 2009: $\beta_0 = -0.107$, $\beta_1 = 0.089$, $r^2 = 0.579$, $P < 0.0001$; 2010, $\beta_0 = -0.058$, $\beta_1 = 0.110$, $r^2 = 0.443$, $P < 0.0001$. Values of $L2_{t+1}$ (white dots) are plotted for 0.1 increments of $\ln$ (males) / trap; however, raw data were used in the analysis.

spruce budworm, average densities of moths and larvae on a per year basis were not significantly correlated for the interval 1992–2010 (Fig. 1), a finding that may seem counterintuitive at first. On the other hand, the expectation of similar temporal variation in numbers of overwintering larvae (L2) and moths ($\male$) between years is based on implicit assumptions about largely inflexible, time-independent larval to moth ratios. Such assumptions are likely not met in all conditions, in particular due to key life-history transitional phases that vary in unpredictable ways from year to year: i) $L2_t \rightarrow \male_t$: mortality of overwintering L2, larval dispersal, parasitism and predation of feeding larvae; ii) $\male_t \rightarrow L2_{t+1}$: sex ratio, male-to-male competitive interactions for access to mate, female reproductive output, adult dispersal, rate of survival or establishment of neonates in overwintering sites.

Captures of males at pheromone traps are also strongly influenced by year-to-year variation in the chemical composition and concentration of lures (Sweeney et al. 1990, Faccioli et al. 1993, Thorpe et al. 1993). The commercial lures used in the current study (Biolure) consist of controlled-release membrane dispersers (bubble of pheromone between two layers of plastic), with an emission rate similar to that of calling females (50–150 ng of pheromone per hour) (Morse et al. 1982, Sanders 1992). Attributes of the Biolure product (purity of pheromone, isomer ratio of E:Z-11-tetradecenal, release rate) were quantified between 1989 and 1991 (Sanders 1992), but unfortunately not thereafter. Year-to-year variations in attributes of Biolure are thus unknown for the interval of the study (1993–2010), even though these variations likely influenced the results in ways that are now impossible to infer, especially because the Biolure product was discontinued in 2010. Ongoing studies

using the lure available since 2011 (Flexlure) aim at quantifying the effects of lure attributes (pheromone load, isomeric ratio) on the derivation of bivariate pheromone-based thresholds.

Within a given year, monitoring of budworms relying on multiyear assessments of larval densities ($L2_t$, $L2_{t+1}$) combined with pheromone trapping ($\male_t$) is justified, as supported by the complementarity (statistical significance) of both $L2_t$ and $\male_t$ in predicting $L2_{t+1}$ for 15 of 18 pairs of 2-yr intervals (Table 1). The bivariate approach developed here further illustrates the quantitative effect of larval densities in parental generations in the derivation of pheromone-based thresholds. Year-to-year noise in larvae-to-moth functions, however, greatly limits the commercial application of the male thresholds derived here; in particular, for larval transitions involving $L2_t = 0$ (Fig. 3). Male thresholds for stable larval population densities ($L2_t = L2_{t+1}$) are more robust, and the following values can be used on an interim basis in the context of EIS: 85 males for $L2_{t+1} = 2$, 130 males for $L2_{t+1} = 3$, 170 males for $L2_{t+1} = 4$, and 205 males for $L2_{t+1} = 5$ (Fig. 3).

One shortcoming of the current study is the relatively low precision level of larval density estimates based on samples of three branches (Sanders 1980). Trade-offs between the cost and precision of operational sampling programs mean that forest managers are unlikely to increase the number of branches per site in the near future. Extensive data sets (such as the one presented here) remain highly valuable research tools—though with potential pitfalls related to imprecise density estimates (Rosenheim and Gratton 2017). These pitfalls may eventually be attenuated by validating pheromone-based thresholds using data from research plots where large number of branches are sampled to estimate larval densities.
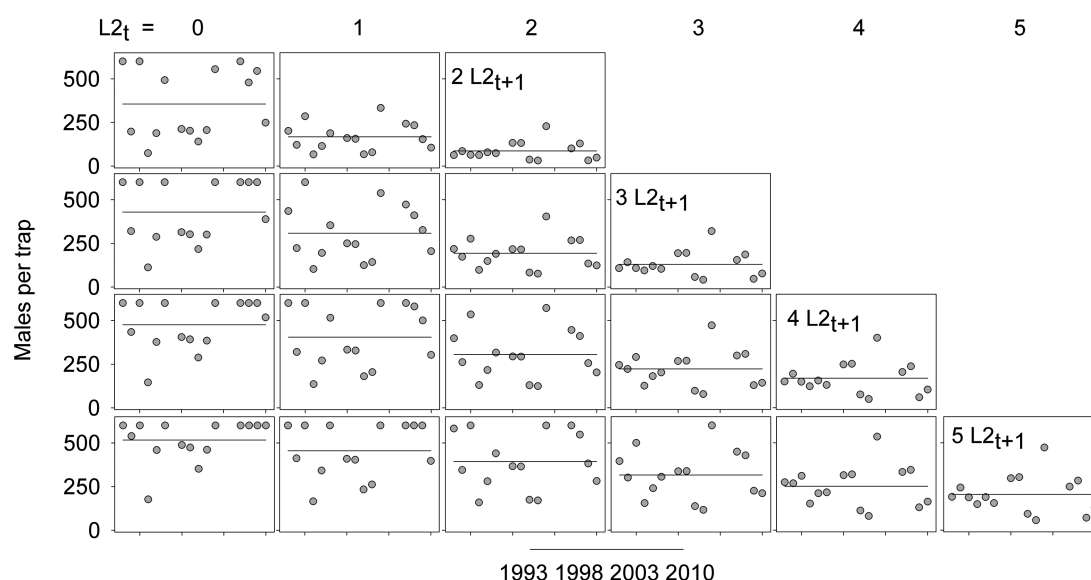
Fig. 3. Pheromone-based thresholds (average number of males per trap) corresponding to different transitions in density of spruce budworm overwintering larvae in parental and offspring generations ($L2_t \rightarrow L2_{t+1}$) as derived for 15 pairs of 2-yr intervals between 1992 and 1993, and 2009 and 2010. Male thresholds were estimated on a per year basis with equation 2, using the parameters reported in Table 1. Thresholds were bounded to a maximum of 600 males because few observations in the data set exceeded this value. The solid line in each plot represents the average threshold per year. Thresholds were not calculated for the intervals 1998–1999, 2004–2005, and 2005–2006 due to overall low larval densities during these years, as well as 'non-sensical' thresholds (>600) exceeding the actual number of males observed.

Acknowledgments

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